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CONTRIBUTIONS IN SCIENCE

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A NEW WALRUS FROM THE IMPERIAL PLIOCENE OF SOUTHERN CALIFORNIA: WITH NOTES ON ODOBENID AND OTARIID HUMERI

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By Edw. D. Mitchell, Jr.[1]

The order Pinnipedia is a taxon representing a number of amphibious mammals derived from an undetermined group of Oligocene Carnivora. This derivation may or may not involve more than one terrestrial assemblage on the family level (see McLaren, 1960). Three well defined families have long been recognized: the Otariidae, eared seals or sea lions; the Odobenidae, walruses; and the Phocidae, true or earless seals. The Otariidae and Odobenidae are grouped in a superfamily, the Otarioidea (Scheffer, 1958), reflecting an early derivation of walruses from sea lions which is documented by good anatomical evidence.

Specimens of extinct otariids have been found only in Tertiary marine deposits of the north Pacific Ocean. Eight genera of these are recognized: *Allodesmus*, *Atopotarus*, *Pontolis*, *Neotherium*, *Desmatophoca*, *Pithanotaria*, *Pliopedia*, and *Dusignathus*. Although many of these sea lions are incompletely known, they all seem to have attained the highly developed structural grade found in living forms.

Heretofore, the record of Tertiary odobenids has been limited to the north Atlantic Ocean: *Prorosmarus alleni* from eastern North America; and two species from Europe, *Alachtherium cretsii* and *Alachtherium antverpiensis*. Ray (1960) has recently summarized evidence which places *Trichecodon huxleyi* in the Quaternary and, on the basis of tusks, extends its range to the Pleistocene of the southeastern United States.

The paleontologic history of otarioid pinnipeds is not well known. *Prorosmarus*, *Alachtherium*, and *Trichecodon* comprise a graded morphologic series of sorts, but critical connecting links are missing between these genera and the primitive otariid-like walrus ancestor. The apparent absence of fossil odobenids from the north Pacific Ocean has long puzzled students of pinniped phylogeny. In attempting to place the ancestral home of the walruses near the center of sea lion evolution, Davies (1958) has assumed that some otariids migrated from the north Pacific Ocean to the Arctic Ocean between middle Oligocene and middle Miocene, and there gave rise to the basic odobenid stock.

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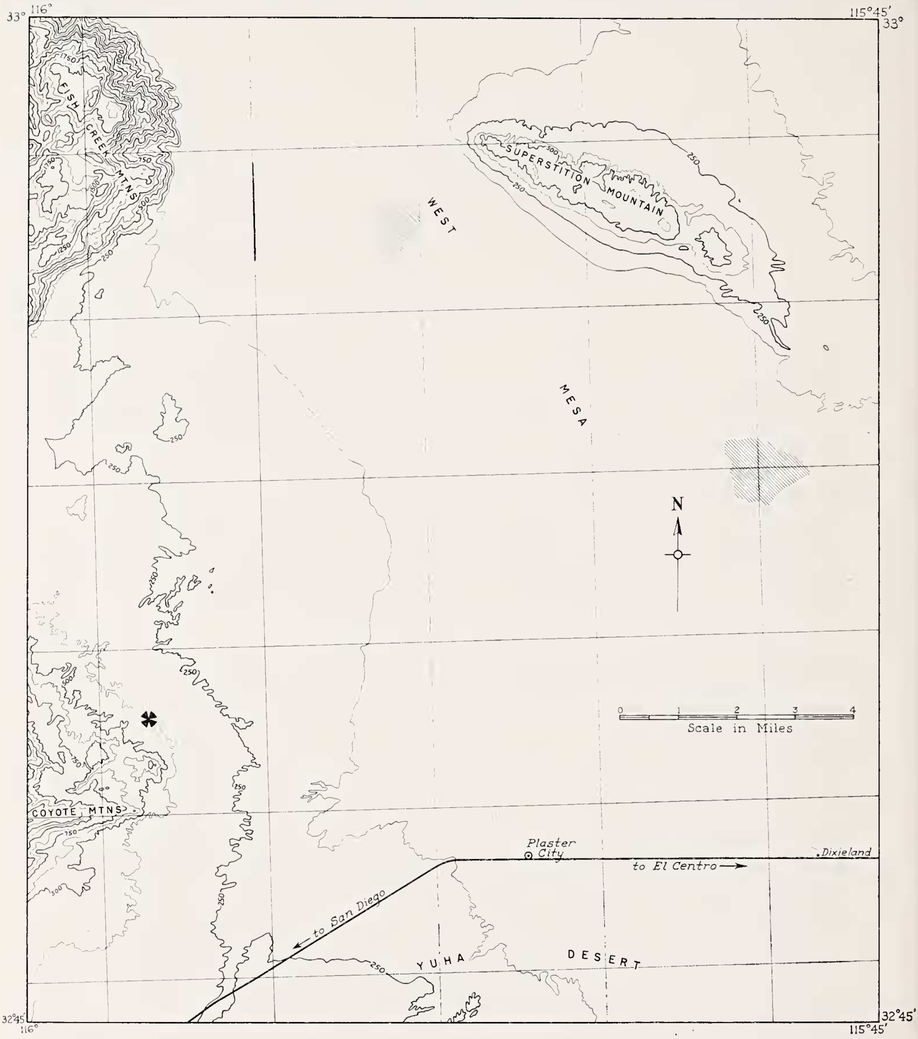

Fig. 1. Map of a portion of western Imperial County, California, showing type locality of *Valenictus imperialensis*, n. gen., n. sp., on the eastern flank of the Coyote Mountains. The map was drawn under the direction of Dr. Chester Stock just prior to his death.

It is, then, significant to report the occurrence of a new walrus in marine sediments exposed on the eastern margin of the north Pacific Ocean, located within the area of Tertiary sea lion radiation. This form is known only on the basis of a single left humerus,[2] but the bone represents an animal so divergent from known pinnipeds that it merits generic, if not familial, recognition. The new genus is tentatively placed in the family Odobenidae on the basis of certain objective odobenid characters. It does not add to our knowledge of walrus evolution, but indicates the diversity of otarioid pinnipeds and demonstrates the multiple pathways utilized in aquatic locomotion by this group.

COMPARATIVE MATERIAL

Humeri of the following living and fossil pinnipeds were examined in this study (numbers following source indicate the number of individuals represented for Recent species, or the catalogue number for particular fossil specimens). Nomenclature of living species follows Scheffer, 1958. The following abbreviations are used: LACM, Los Angeles County Museum; USNM, United States National Museum; DRD, Donald R. Dickey Collection, University of California, Los Angeles; and OSC, Oregon State College. LACM (CIT) refers to the vertebrate paleontology collection of the California Institute of Technology, now in the Los Angeles County Museum.

OTARIIDAE. LIVING SPECIES: *Otaria byronia* (cast), LACM, 1; *Eumetopias jubata*, LACM, 2, DRD, 2; *Zalophus californianus californianus*, LACM, 8; *Arctocephalus philippii townsendi*, LACM, 16; *Callorhinus ursinus*, LACM, 3. (See figs. 8, 9)

OTARIIDAE. FOSSIL SPECIES: *Allodesmus kernensis*, LACM 1404, 4320; *Atopotarus courseni*, LACM 1376; cf. *Pontolis magnus*, LACM 4324; cf. *Neotherium*, LACM 4319; cf. *Desmatophoca oregonensis*, OSC V-822. (See figs. 10, 11) Dr. Warren Freihofer of Stanford University informs me (*in litt.*) that the type specimens of *Pliopedia pacifica* and *Pithanotaria starri* are lost in the Museum at Stanford. The referred specimen of *Pithanotaria starri* described with the type is not available to me. The humerus of *Dusignathus santacruzensis* is not known.

ODOBENIDAE. LIVING SPECIES: *Odobenus rosmarus rosmarus*, USNM, 1; *Odobenus rosmarus divergens*, USNM 4, DRD, 1. (See figs. 12, 13)

ODOBENIDAE. FOSSIL SPECIES: *Alachtherium cretsii* (cast), USNM 11788; *Trichecodon huxleyi* (cast), USNM 11786. (See figs. 12, 13)

PHOCIDAE. LIVING SPECIES: *Phoca vitulina richardi*, LACM, 4; *Pusa hispida ochotensis*, USNM, 1; *Pagophilus groenlandicus*, USNM, 1; *Halichoerus grypus*, USNM, 1; *Erignathus barbatus*, USNM, 1; *Monachus*

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[2] The late Dr. Chester Stock, former Chief Curator of Science at the Los Angeles County Museum and Chairman of Geology, California Institute of Technology, recognized the affinities of the specimen herein described, but at the time of his death he had completed only a few preliminary notes pertaining to the fossil humerus.

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schauinslandi, USNM, 1; *Lobodon carcinophagus*, USNM, 1; *Ommatophoca rossi*, USNM, 1; *Hydrurga leptonyx*, USNM, 1; *Cystophora cristata*, USNM, 1; *Mirounga angustirostris*, LACM, 6.

Order *PINNIPEDIA* Illiger, 1811
Superfamily OTARIOIDEA Smirnov, 1908
Family **Odobenidae** Allen, 1880
Genus *Valenictus* n. gen.

TYPE SPECIES. *Valenictus imperialensis* n. sp. (figs. 2-4)

ETYMOLOGY. *valens* (from *valeo*): strong, powerful; *ictus*: a stroke or thrust; *imperialensis*: after Imperial County, California.

HOLOTYPE. LACM (CIT) 3926: A nearly complete left humerus lacking only the distal external half of the lateral (radial) capitulum; some thin flakes of lamellar surface of shaft and distal end chipped or cracked off, but conformation and texture of bone evident; proximal epiphyseal suture still showing as traceable groove; collected by Mr. Royal S. Foote, 1949.

TYPE LOCALITY. LACM (CIT) 472, 1000 feet south, 800 feet east of northwest corner, Sec. 32, T. 15 S., R. 10 E., Painted Gorge Quadrangle, California, USGS 1957: On the 400 foot elevation contour in the mouth of Painted Gorge, eastern flank of Coyote Mountains, Imperial County, California (Fig. 1).

FORMATION AND AGE. In reef bed of small *Ostrea* sp., *Anomia* sp., occasional *Pecten* sp., the bed occurring in siltstones (which lie in Capote member of Christensen's [1957, pls. 1, 3] differentiation of Imperial formation in Coyote Mountain region) of Imperial formation; best considered early Pliocene in age (Durham, 1954, p. 27). Dr. Chester Stock visited this locality with Mr. Arthur Hicks and Mr. Royal S. Foote on 24 September 1949. Accompanied by Mr. Jere H. Lipps, I visited the locality twice (26, 27 June 1960; 7 November 1960). Extensive prospecting and quarrying revealed no additional vertebrate remains. Only one other vertebrate (*Carcharodon arnoldi* Jordan) is known from area, and this on the basis of a single tooth (Hanna, 1926, p. 483, pl. 23, fig. 7).

DIAGNOSIS OF GENUS. Capitulum small, the greatest transverse diameter 27% of length of humerus from capitulum to most proximal concavity of trochlea, the capitular axis-shaft axis angle 20°; greater tuberosity of same height as capitulum; lesser tuberosity lower than capitulum, round in cross section; deltoid crest broad, as measured anterolaterally, culminating in a greatly developed deltoid tuberosity, the crest extending distally to the level of the dorsal border of entepicondyle; bicipital groove narrow, with steep sides; posterior border of shaft essentially straight; entepicondyle large, placed distally, accounting for almost one-half the total distal width; principal transverse axis of distal end forming an acute interior angle of 70° with vertical axis of shaft.

Diagnosis of species. Same as that of the genus until further species are described.

Comparisons With Living Pinnipeds

Distinctions from the Phocidae are so clearly marked that it is unnecessary to include discussion of members of this family here. *Eumetopias jubata* (LACM M550) and *Odobenus rosmarus divergens* (USNM 200336) are selected as typical representatives of the Otariidae and Odobenidae, respectively, with which to compare the fossil.

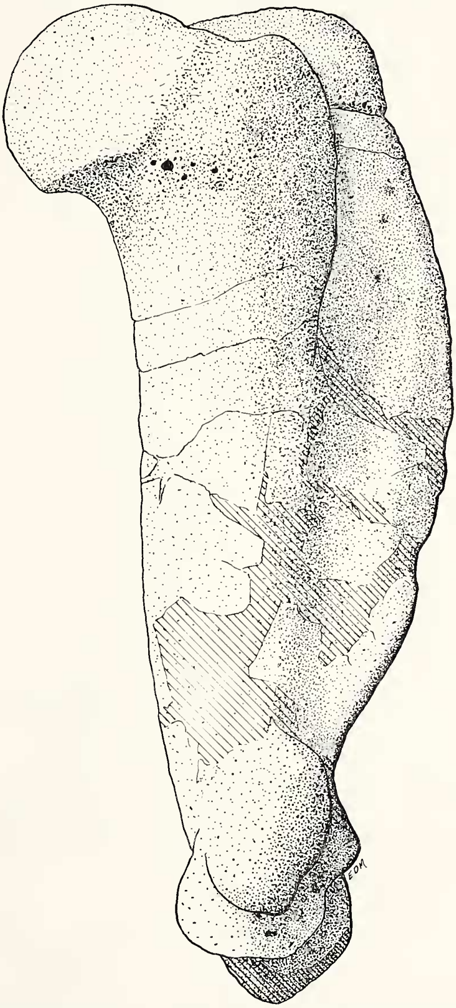


Fig. 2. *Valenictus imperialensis*, n. gen., n. sp., holotype, LACM (CIT) 3926. Medial view of left humerus, one-half natural size. Locality LACM (CIT) 472, early Pliocene, Imperial formation, Coyote Mountain region, Imperial County, California.

In general proportions the humerus of *Valenictus* is relatively more massive than that of either *Eumetopias* or *Odobenus,* though in length the fossil is shorter than both (see figs. 8, 9, 12, 13). The fossil bone represents a young adult, for the proximal epiphyseal suture is still visible; no distinct suture shows in the specimens of the two living genera. The capitulum is relatively smaller in *Valenictus,* the greatest transverse diameter being 27% of the functional length, and it is connected to the

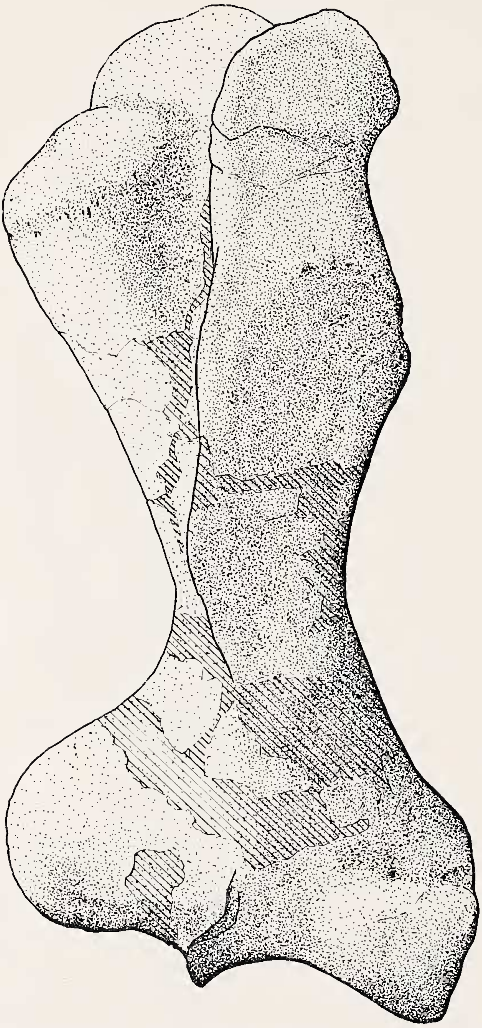


Fig. 3. *Valenictus imperialensis,* n. gen., n. sp., holotype, LACM (CIT) 3926. Anterior view of left humerus, one-half natural size. Locality LACM (CIT) 472, early Pliocene, Imperial formation, Coyote Mountain region, Imperial County, California.

lesser tuberosity by a thick, high ridge. This capitular diameter-functional length ratio is 31% in *Odobenus,* and the ridge is lower; in *Eumetopias* the ratio is 38%, and the ridge is similar to *Valenictus.* The lesser tuberosity in *Valenictus* is lower than the capitulum, round in cross section, and in dorsal view lies more mediad; in *Odobenus* it is lower than the capitulum, elongate anterolaterally in cross section, and lies more anteriorly in dorsal view; in *Eumetopias* it is also lower than the capitulum, round in cross section, and lies anteromedially. In dorsal view the greater tuberosity in *Valenictus* extends anteriorly and then is inflected anteromedially, and the deltoid crest is essentially uniform in cross section for the majority of its length; in *Odobenus* the tuberosity is similar and more highly developed, the medial inflection extending almost at right angles to the deltoid wall for 12 mm., and the crest is uniform down its length; *Eumetopias* differs in having a rounded greater tuberosity, and a transversely expanded deltoid crest which folds over the bicipital groove internally and the gutter of the brachialis and supinator muscles externally. In lateral view the deltoid crest in *Valenictus* extends distally to the proximal border of the entepicondyle, describes an arc with a radius of 15 cm. running from the greater tuberosity to the coronoid fossa, is thickened, and gently grades into the shaft distally; in *Odobenus* it does not extend to the entepicondyle, is straight proximally, thin and sharp-edged distally, and drops to the shaft abruptly at the distal end. The deltoid tuberosity in *Valenictus* is well developed, and a ridge extends from this tuberosity to the distal extremity of the deltoid crest; in *Odobenus* the same conditions hold; but in *Eumetopias* the ridge, running between the insertions of the deltoid and brachialis muscles, forms the external flange of the deltoid crest. In lateral view the posterior border

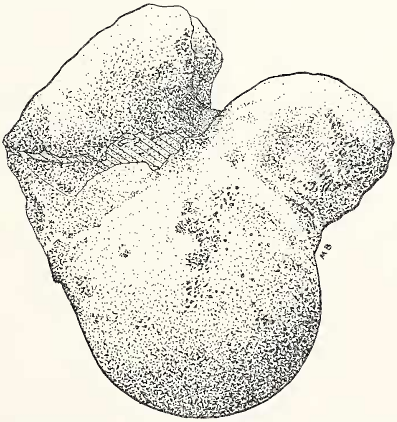


Fig. 4. *Valenictus imperialensis,* n. gen., n. sp., holotype, LACM (CIT) 3926. Proximal view of left humerus, one-half natural size. Locality LACM (CIT) 472, early Pliocene, Imperial formation, Coyote Mountain region, Imperial County, California.

of the shaft in *Valenictus* is essentially straight, the capitulum projects posteriorly only 3.2 cm., and the capitular axis is directed dorsoposteriorly from the axis of the shaft at an angle of 20°; in *Odobenus* the posterior border of the shaft is gently curved, the capitulum projects back 7.5 cm., and the capitulum axis-shaft axis angle is 40°; in *Eumetopias* the posterior border of the shaft is markedly sigmoid, the capitulum projects posteriorly 6 cm., and the capitular axis-shaft axis angle is also 40°. The coronoid fossa in *Valenictus* is shallow, and not distinctly set off from the surrounding articular and shaft surfaces; in *Odobenus* it is broad and shallow (5 mm. deep); in *Eumetopias* it is deeper, 9 mm. lower than the surface of the trochlea. The entepicondyle in *Valenictus* is large, massive, well rounded, and projects very far mediad; in *Odobenus* it is large, subtriangular, but does not project as far mediad; in *Eumetopias* it is large, less massive, well rounded, and does not project as far mediad. An entepicondylar foramen may or may not be present in the *Valenictus* humerus, for a small area in which it might have occurred is shattered and lost; this foramen is not found in *Odobenus* or *Eumetopias*. It is questionable in *Valenictus* whether the ectepicondyle extends farther laterally than the radial capitulum or not, for this area was lost and has been restored; this condyle extends beyond the radial capitulum in both *Odobenus* and *Eumetopias*. In *Valenictus* the trochlear surface for the ulna is weakly concave in the transverse plane, does not extend up the anterior face of the shaft very far (2.5 cm.), and the medial edge of the trochlea is weakly developed (extending distally beyond the entepicondyle 1.0 cm.); in *Odobenus* the trochlear surface is more strongly concave, extends relatively farther up the shaft, and the medial edge is very strong; in *Eumetopias* the trochlear surface is very concave and robust, and the medial edge is even stronger.

The humeri of *Zalophus* and *Otaria* (figs. 8, 9) closely resemble that of *Eumetopias* (see fig. 5), differing only in minor details which do not affect the above comparison of the fossil humerus with *Eumetopias*. Humeri of *Arctocephalus* and *Callorhinus* (figs. 8, 9) differ, among other characters, in having a high, delicate greater tuberosity, thin deltoid crest, S-shaped posterior border of the shaft, and in being about one-half the length of the fossil humerus. Both of these genera resemble *Valenictus* in the possession of a relatively small capitulum, and a small capitular axis-shaft axis angle.

The variation plotted in figure 5 of fourteen humeral characters in five genera of Recent otariids can be in large part attributed to age and sex differences. Sexual differences are generally manifest in size disparity. Age differences, of course, account for a wide size range and changes of relative proportions between structures on the humeri of very young and very old specimens of a given species. The magnitude of the above variations, even considering a set of extreme values, is not sufficient to account for the structural peculiarities of the *Valenictus* humerus. *Eume-*

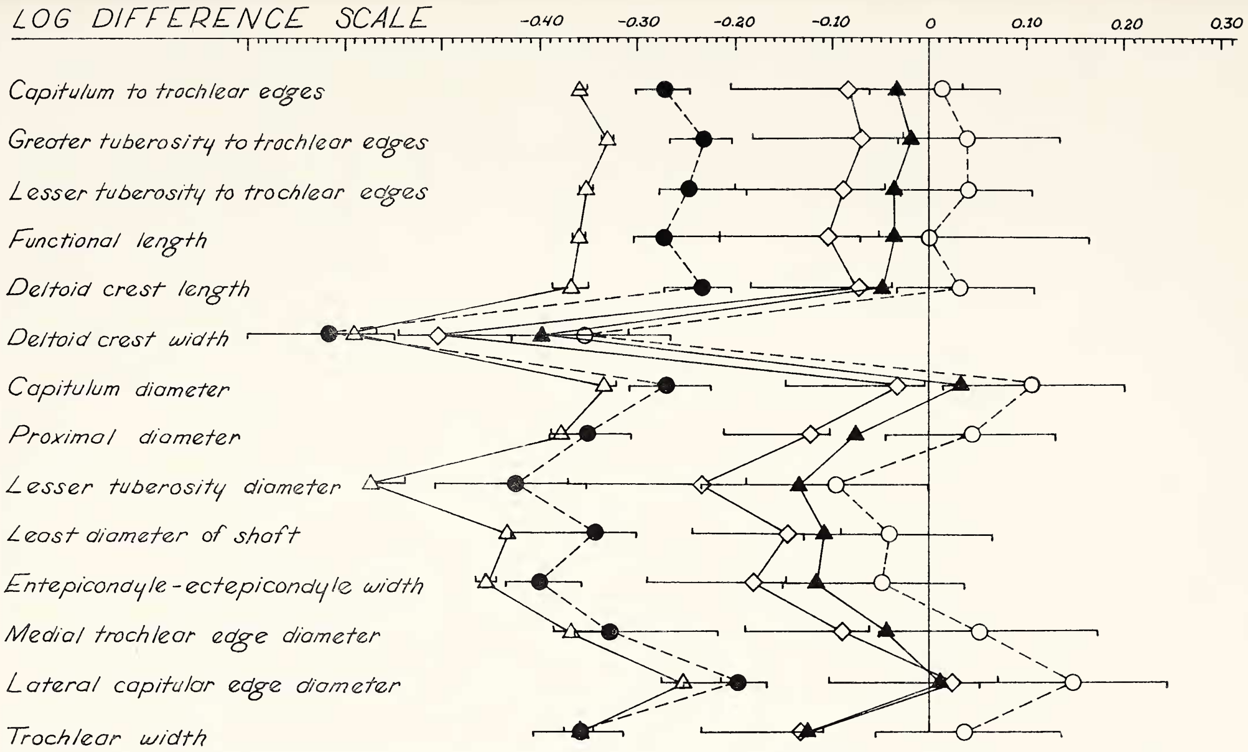


Fig. 5. Ratio diagram of dimensions of Recent otariid humeri. The open triangles represent a sample of 3 *Callorhinus* humeri; the solid circles a sample of 16 *Arctocephalus* humeri; the open diamonds a sample of 8 *Zalophus* humeri; the solid triangles represent a single *Otaria* humeral cast; and the open circles a sample of 4 *Eumetopias* humeri. The above numbers refer to the number of individuals represented. The symbols denote the arithmetical mean, the horizontal lines the observed range. The measurements are more fully explained in Table 1. No vertical scale is used. The horizontal scale represents the logarithm of the deviation from the *Valenictus imperialensis* humerus for each of fourteen humeral measurements.

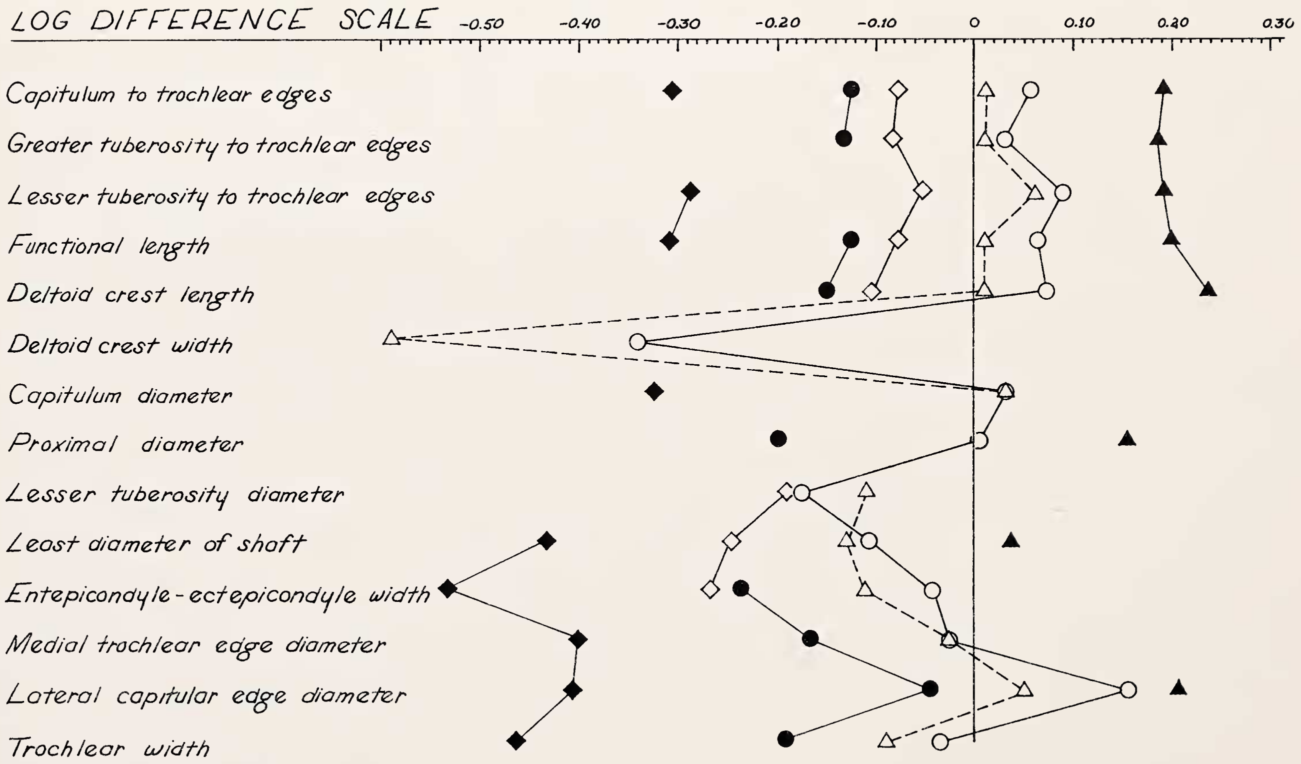


Fig. 6. Ratio diagram of dimensions of fossil otariid humeri. The following symbols are used: Solid triangles for cf. *Neotherium*, LACM 4319; solid circles for *Atopotarus*, LACM 1376; open diamonds for cf. *Desmatophoca*, OSC V-822; open triangles for *Allodesmus*, LACM 1404; open circles for *Allodesmus*, LACM 4320; and solid triangles for cf. *Pontolis*, LACM 4324. See fig. 5 for explanation of diagram.

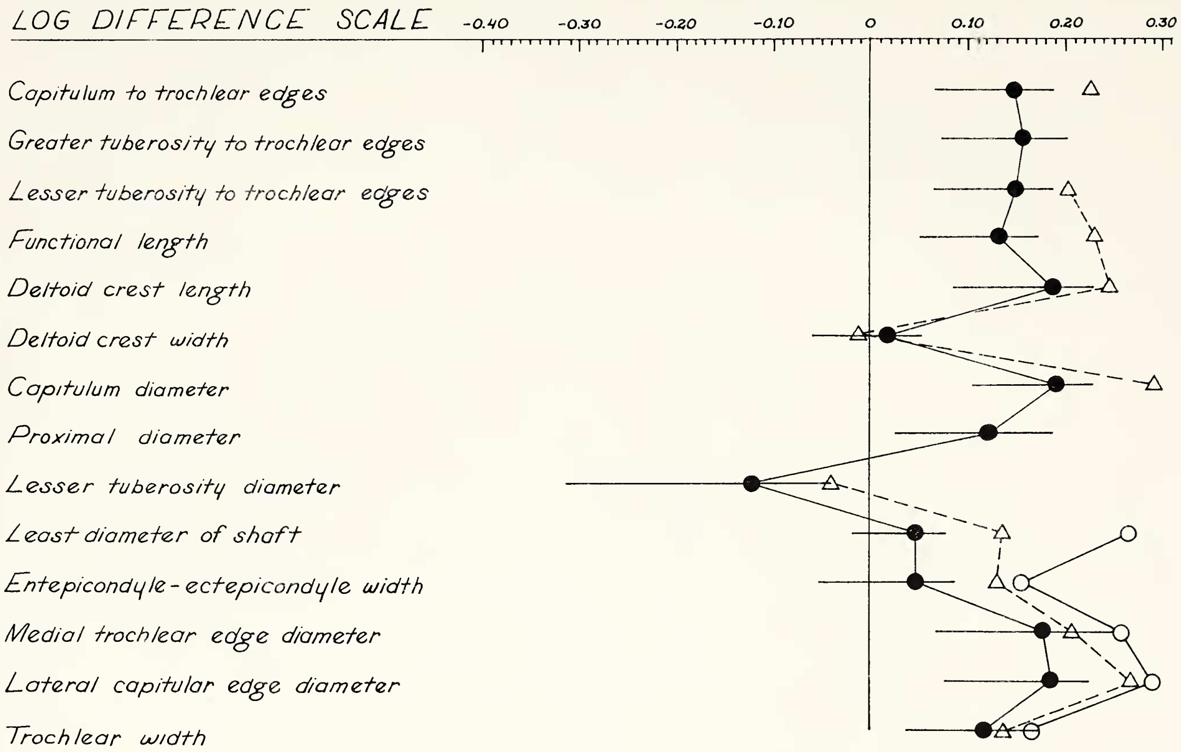
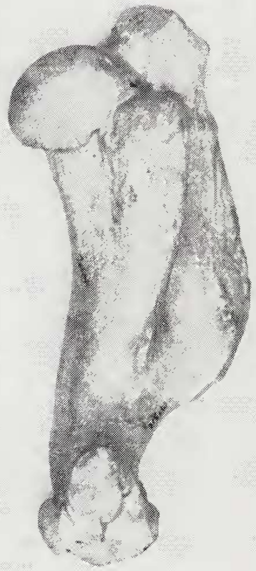


Fig. 7. Ratio diagram of dimensions of Recent and fossil odobenid humeri. The following symbols are used: solid circles for a sample of 5 *Odobenus* humeri; open triangles represent an *Alachtherium* humeral cast, USNM 11788; and the open circles a humeral cast of *Trichecodon*, USNM 11786. See fig. 5 for explanation of the diagram.



topias approximates *Valenictus* more closely than other otariids in many characters, including absolute size. These resemblances, however, are probably convergent. In many characters (narrowness of bicipital groove, straightness of posterior border of shaft, and the entepicondyle accounting for almost one-half of extreme width at distal end, to name just a few) the new genus lies far beyond even the extremes of these characters in all other otarioid genera.

Comparisons With Fossil Pinnipeds

Otariidae

Allodesmus kernensis Kellogg, 1922.—Comparison with an excellently preserved humerus of this species (LACM 4320, figs. 10, 11) from the type locality at Sharktooth Hill and a humerus (LACM 1404) correctly referred to this genus (see fig. 6) by Downs (1955) emphasizes the extreme specialization of the *Valenictus* humerus. The most obvious characters differentiating the new genus from *Allodesmus* are as follows: Increased diameter of the lesser tuberosity, thickening of the already large entepicondyle, reduction in the size of the distal articular surfaces, thickening of the deltoid crest externally, increase in diameter proximally and overall shortening of the shaft, and reduction in the diameter of the proximal capitulum.

Atopotarus courseni Downs, 1956.—Virtually no critical differences were found between humeri of *Atopotarus courseni* (Downs, 1956, fig. 3) and *Allodesmus kernensis*. Comparison of humeral measurements on a logarithm difference scale (see fig. 6) shows the proportions to be identical. Since the only difference observed was that of size (see table 1) further discussion is omitted here.

Pontolis magnus True, 1905 (also True, 1909).—The type specimen of this species is a skull, but Lyon (1941) has referred a distorted partial skeleton to the same species. Through the courtesy of Dr. Peter P. Vaughn, the previously uncatalogued specimen reported on by Lyon has been obtained by the Los Angeles County Museum and is now LACM 4324. Further preparation of the laterally crushed humerus of this specimen (fig. 10) shows the presence of the following characters which serve to distinguish it from the *Valenictus* humerus: Humerus longer (resembling that of *Allodesmus*); deltoid crest probably thinner (as in *Allodesmus*); deltoid tuberosity absent; and distal articular surfaces evidently well developed, with sharp capitular and trochlear edges (as in *Eumetopias*). No more can be stated positively with regard to this poorly preserved specimen, but overall proportions alone are enough to distinguish it from *Valenictus*.

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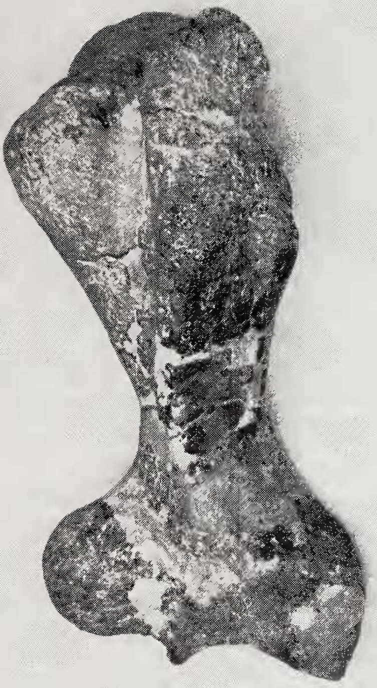
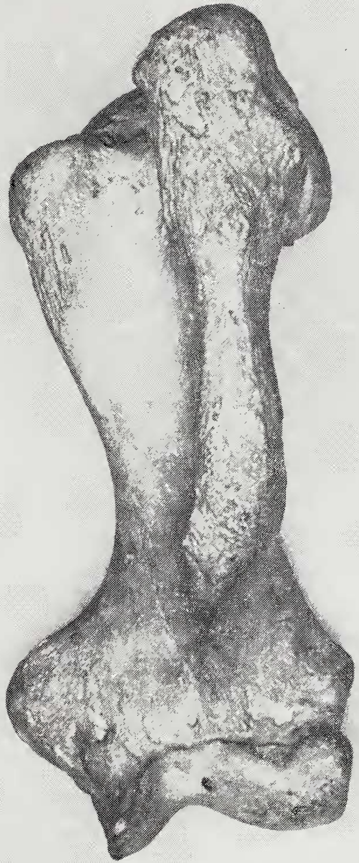
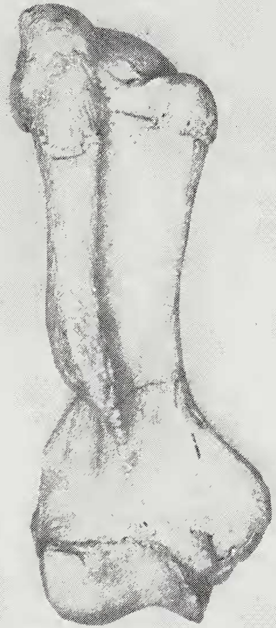
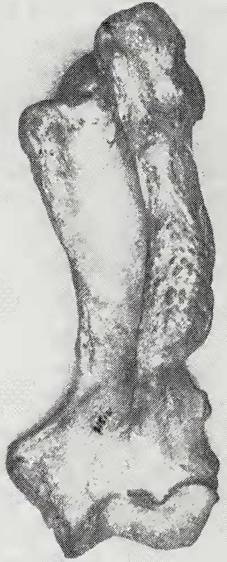
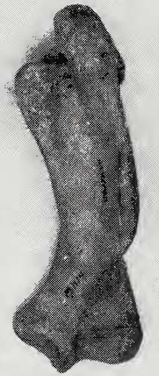
Fig. 8. Medial views (top to bottom) of left humeri of *Valenictus imperialensis*, n. gen., n. sp., LACM (CIT) 3926; *Eumetopias jubata*, LACM M550; right humerus of *Otaria byronia*, LACM M1611, cast; left humeri of *Zalophus californianus*, LACM M1318; *Arctocephalus philippii townsendi*, LACM M1114; and *Callorhinus ursinus*, LACM M1502. All approximately one third natural size. Photograph by Armando A. Solis.

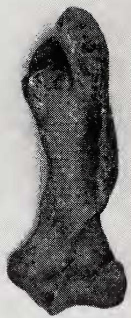












Neotherium mirum Kellogg, 1931.—The only humeral material heretofore referred to this genus is a proximal end fragment. A small, nearly complete left humerus (LACM 4319, figs. 10, 11) may be referable to this genus, for it is from the type locality (Sharktooth Hill) and differs considerably from *Allodesmus,* among other characters, in its smaller size and arcuate shaft. The specimen is, however, at variance with Kellogg's description of the proximal end fragment (1931, p. 297) in that the anterior border of the deltoid crest folds over the external surface of the crest as in *Zalophus.* The cf. *Neotherium* designation here placed on this humerus (LACM 4319) is necessarily tentative, for Kellogg himself (1931, p. 227) felt that at least one other pinniped occurs in the Sharktooth Hill fauna. This view seems to be supported by certain elements not referable to either *Allodesmus* or *Neotherium* recently collected from the type locality by the Los Angeles County Museum. *Valenictus* is quite distinct from this humerus (LACM 4319), which has (in comparison with the *Valenictus* humerus): a long, slender, externally bowed shaft; small, deep olecranon fossa; thin deltoid crest; relatively large proximal capitulum; and a well defined coronoid fossa.

Desmatophoca oregonensis Condon, 1906.—The pinniped humerus referred to this species by Packard (1947) has since been catalogued as OSC V-822. This left humerus (figs. 10, 11; not the right as stated by Packard) differs markedly from *Valenictus* in having a thin deltoid crest, a more slender and lightly constructed shaft which is bowed laterally, a concavely curved posterior border of the shaft, and a relatively small entepicondyle. The entire shaft of OSC V-822 (cf. *Desmatophoca*) seems to be longitudinally sculptured in response to stress. The posterior face of the shaft between the capitulum and lesser tuberosity is well excavated, leaving a prominent ridge running more than half way down the shaft from the lesser tuberosity. The bicipital groove is distally widened and excavated, accentuating this ridge below the lesser tuberosity. Packard's figures of this humerus (1947, pl. 3) are mislabeled, and this must be kept in mind while reading the description. For his figure 1 caption, read 'lateral aspect' for 'anterior aspect', and for figure 2, read 'medial' for 'posterior.' Reference to measurements (1947, p. 26) show that the figures are not natural size but three quarters natural size. Definite similarities are seen in the humerus from Oregon referred to *Desmatophoca* and that from Sharktooth Hill referred to *Neotherium.* Both exhibit a greater degree of torsion than found in other fossil otariid genera. The Oregon specimen is 40% longer, but comparable structures are in agreement. The differences observed in figure 6 between these two specimens

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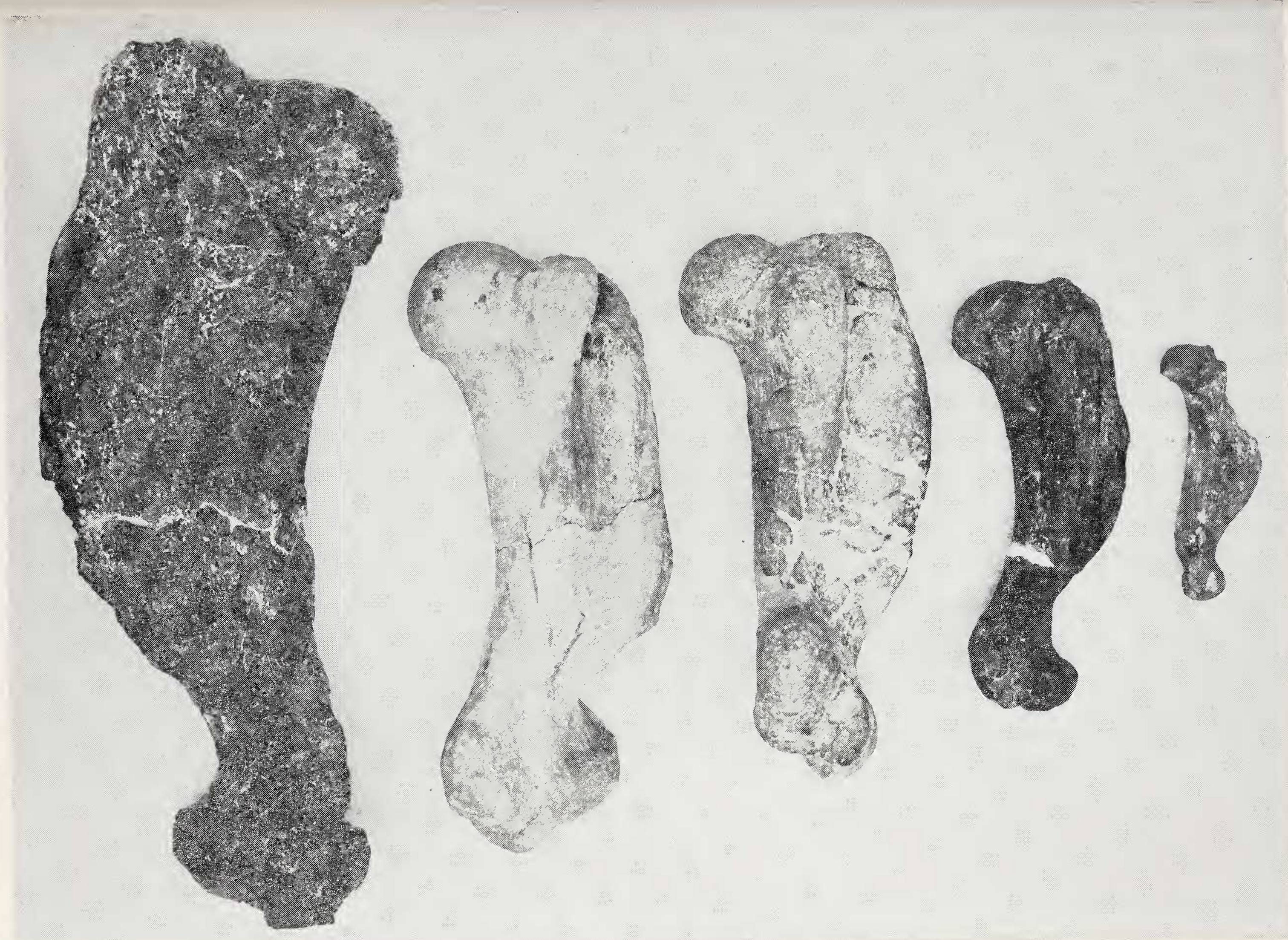
Fig. 9. Anterior views (top to bottom) of left humeri of *Valenictus imperialensis,* n. gen., n. sp., LACM (CIT) 3926; *Eumetopias jubata,* LACM M550; right humerus of *Otaria byronia,* LACM M1611, cast; left humeri of *Zalophus californianus,* LACM M1318; *Arctocephalus philippii townsendi,* LACM M1114; and *Callorhinus ursinus,* LACM M1502. All approximately one third natural size. Photograph by Armando A. Solis.



may be due in part to the poor preservation of the Oregon humerus. For this reason, definite conclusions cannot be reached.

Pithanotaria starri Kellogg, 1925.—The humerus of *Pithanotaria* (observed only from the illustrations, 1925, figs. 1, 2; pl. 12) differs from that of *Valenictus* in having a small entepicondyle, a thin and flaring supinator ridge, a large radial capitulum, an overrolling of the exterior margin of the deltoid crest, and a relatively straight anterior margin of the deltoid crest (similar to that in *Allodesmus* and *Atopotarus*).

Pliopedia pacifica Kellogg, 1921.—The humerus of this species (as observed in the type illustration, 1921, fig. 1) is much more lightly constructed, with a thinner shaft than that of *Valenictus*; the deltoid crest is thinner, and its anterior border is much straighter and drops abruptly to the shaft distally; the coronoid fossa appears to be larger and deeper; the entepicondyle is subtriangular rather than round; the distal trochlear surface is relatively larger; and the supinator ridge is thinner and pronounced.

Dusignathus santacruzensis Kellogg, 1927.—Unfortunately, *Dusignathus* is known only from cranial elements (Kellogg, 1927, figs. 1-6) and cannot be compared with *Valenictus* at the present time.

The above comparison of the humerus of *Valenictus imperialensis* with those of known fossil otariids has eliminated any possibility that *Valenictus* might be placed in this family. In none of the otariid genera is a deltoid tuberosity to be found, nor do capitular, entepicondylar, or shaft characters coincide with any otariid. In addition, this survey has shown the humeri of *Allodesmus* and *Atopotarus* to be similar, suggesting a close phyletic relationship. The same may be said for a relationship between LACM 4319 (cf. *Neotherium*) and OSC V-822 (cf. *Desmatophoca oregonensis*), both of which follow a basic structural plan and are similar in spite of marked size differences (see table 1 and fig. 6).

Odobenidae

Alachtherium cretsii Du Bus, 1867.—The humerus of this species (cast, USNM 11788; figs. 12, 13; see also Beneden, 1877, pl. 3, figs. 1, 2; pl. 4, figs. 1, 2) differs from that of *Valenictus* in the following characters: The greater tuberosity is higher than the capitulum; the lesser tuberosity is less massive and not round in cross section; the bicipital groove is wide; the capitulum is larger; the posterior border of the shaft is curved; the entepicondyle is smaller and differs in shape; the deltoid crest is more linear in lateral view; and the capitulum diameter-functional length ratio is larger than in *Valenictus*. The *Alachtherium* humerus bears a very close resemblance to that of *Odobenus* (see fig. 7).

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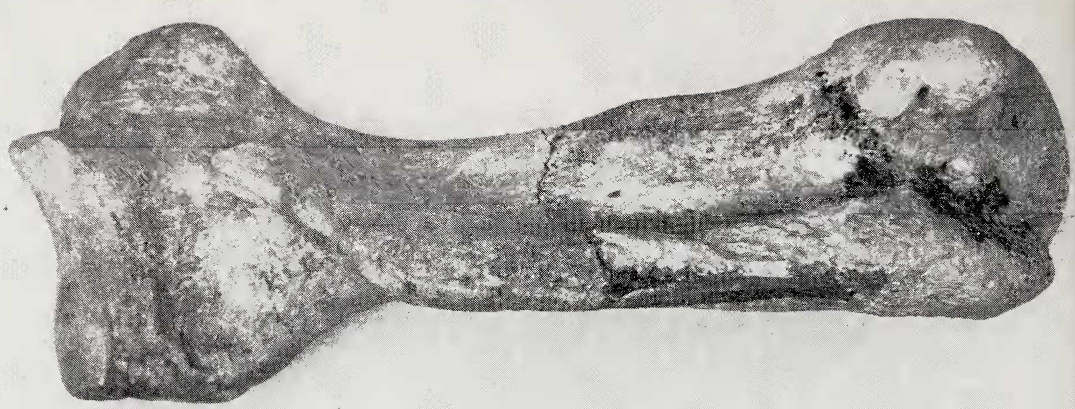
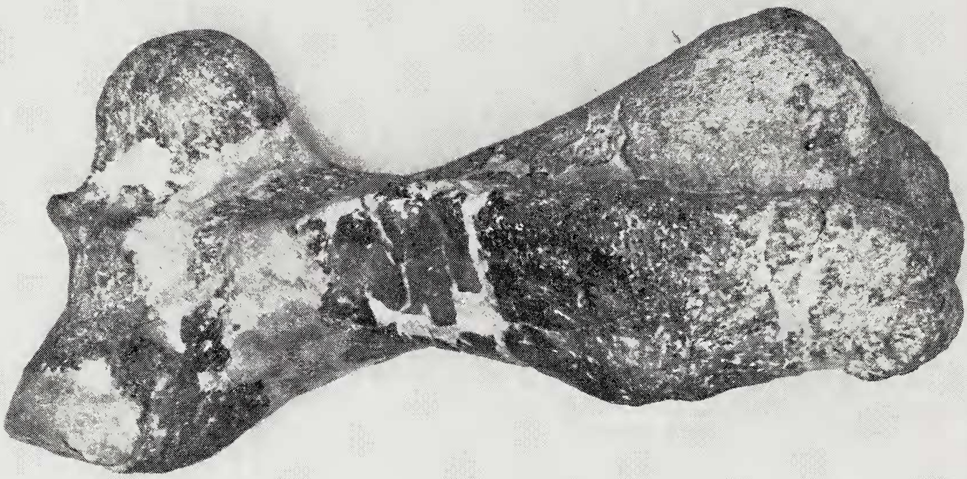
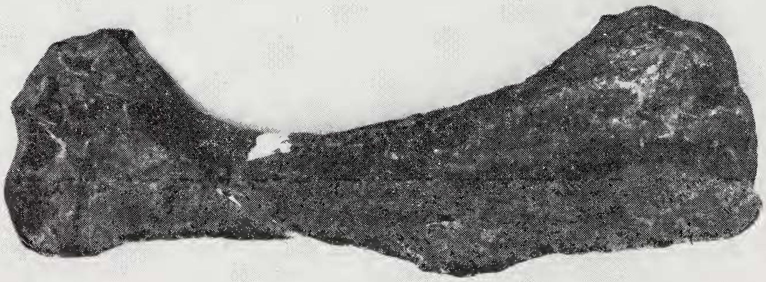
Fig. 10. Medial views (top to bottom) of right humerus of cf. *Pontolis magnus*, LACM 4324; left humeri of *Allodesmus kernensis*, LACM 4320; *Valenictus imperialensis*, n. gen., n. sp., LACM (CIT) 3926; cf. *Desmatophoca oregonensis*, OSC V-822; and cf. *Neotherium*, LACM 4319. All somewhat more than one third natural size. Photograph by Armando A. Solis.







The condition of the deltoid tuberosity in the humerus of *Alachtherium* presents an interesting intermediate structural grade between that seen in *Odobenus* and *Valenictus* on one hand and the condition existing in *Eumetopias* and other otariids on the other. In *Alachtherium*, the posterior border of this tuberosity is elevated from the shaft and continuous with the posterolateral margin of the deltoid crest. In *Eumetopias*, the deltoid tuberosity is lost, being consolidated with the anterior surface of the deltoid crest. In *Odobenus* and *Valenictus* the tuberosity has pulled away from the deltoid crest and 'migrated' posterolaterally, being situated much more proximally in *Valenictus* than in *Odobenus*. In these two genera the tuberosity is a swelling continuous with both the shaft and crest surfaces.

Trichecodon huxleyi Lankester, 1865.—A humeral fragment (cast, USNM 11786, figs. 12, 13; see also Beneden, 1877, pl. 7, figs. 1, 2; pl. 8, figs. 1, 2) of *Trichecodon huxleyi* (=*T. koninckii*) differs from the *Valenictus* humerus in the possession of a wide, deep, and well delineated olecranon fossa; a smaller, rugose, and posterodorsally inflected entepicondyle; larger, more fully rounded distal articular surfaces set off distinctly from the shaft; a deeper coronoid fossa; a large rugose ectepicondyle; and a well developed supinator crest. The *Trichecodon* humerus is very similar to that of *Odobenus* (see fig. 7).

Prorosmarus alleni Berry and Gregory, 1906.—This genus and species was described on the basis of a mandibular ramus (Berry and Gregory, 1906, figs. 1, 4), and thus far no postcranial bones have been found.

Odobenus, *Trichecodon*, *Alachtherium*, and *Prorosmarus* are all closely allied odobenid genera, and *Valenictus* may be considered a more divergent form set somewhat apart from the typical Odobenidae. *Alachtherium* and *Trichecodon* humeri are quite similar to the humerus of *Odobenus*, although the diagnostic odobenid humeral character, the deltoid tuberosity, is structurally intermediate in *Alachtherium* between the conditions in *Eumetopias* and *Odobenus*.

DISCUSSION

The *Valenictus imperialensis* humerus is essentially that of a primitive otarioid pinniped, but has a number of striking specializations superimposed on this plan, and these somewhat obscure its basic form.

Even though very much shortened, the *Valenictus* humerus still retains the primitive, straight posterior border of the shaft. The small capitular axis-shaft axis angle indicates that the humerus was normally carried in a position of lesser flexure relative to the scapula. This angle is 20° in *Valenictus*, being smaller than that in any other otarioid, living or fossil.

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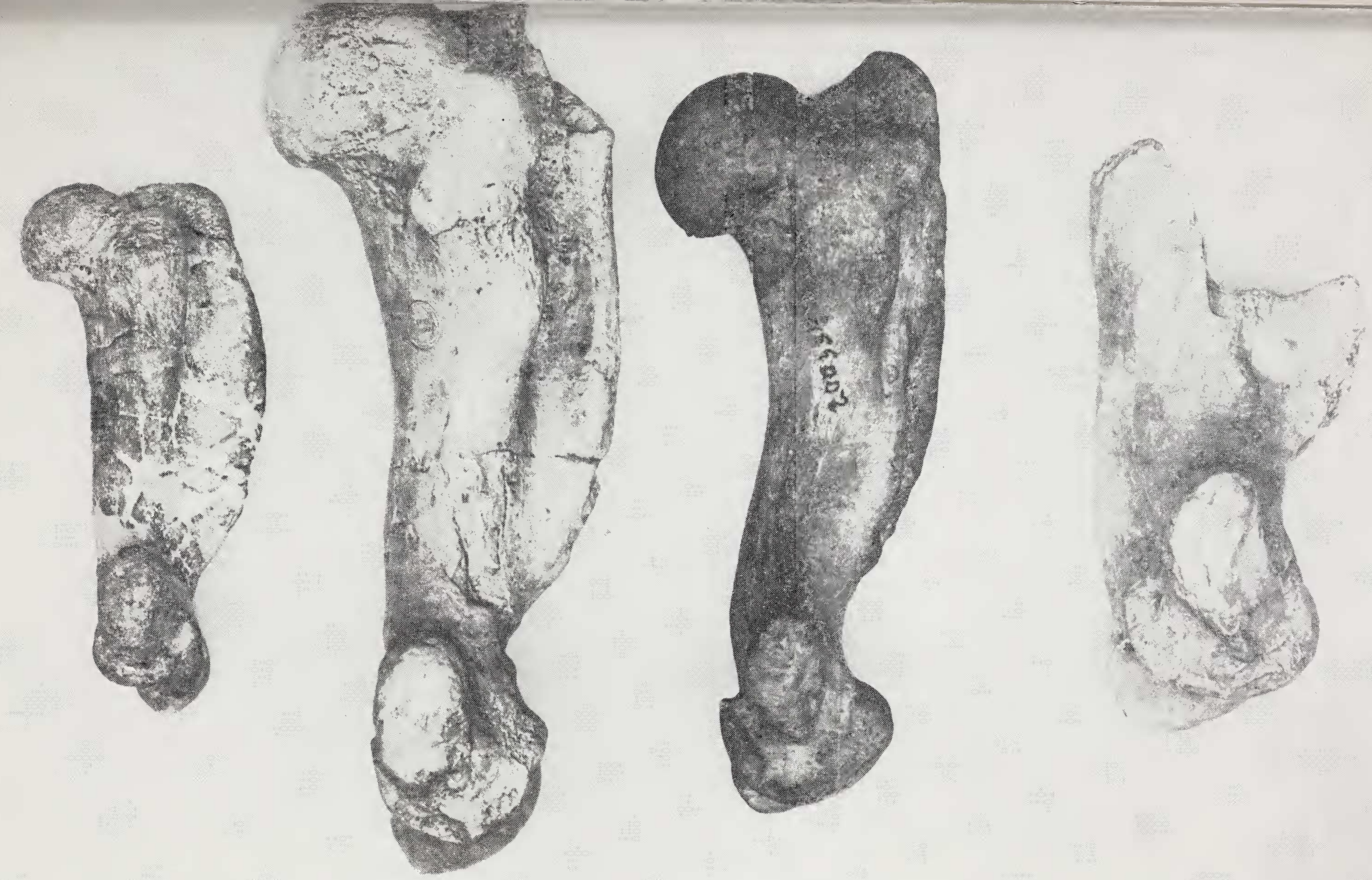
Fig. 11. Anterior views (top to bottom) of left humeri of *Allodesmus kernensis*, LACM 4320; *Valenictus imperialensis*, n. gen., n. sp., LACM (CIT) 3926; cf. *Desmatophoca oregonensis*, OSC V-822; and cf. *Neotherium*, LACM 4319. All a little less than one half natural size. Photograph by Armando A. Solis.



Downs (1956, p. 130) found this angle to be between 30° and 40° in five genera of Miocene otariids. My findings, supplementing those of Downs, are based on only one specimen per genus, and are as follows: *Allodesmus* (36°), cf. *Neotherium* (LACM 4319, 26°), *Arctocephalus* (39°), *Callorhinus* (35°), *Zalophus* (36°), *Eumetopias* (40°), and *Otaria* (40°). *Odobenus* (40°) does not differ significantly from the above genera, but *Valenictus* is the only otarioid having an angle less than 30°, excepting the cf. *Neotherium* specimen. This small angle is a primitive character in the Otariidae (Downs, 1954). The lowness of the greater tuberosity does not imply a weakness in the muscles concerned with its development, for the tuberosity is massive, rugose, and occupies nearly the same shape and anterior position on the humeral shaft as in *Odobenus*. Its height can be in part attributed to a selection for more power through the return stroke of the brachium, and the resulting elongation of the supraspinatus muscle. Downs (1954) states that a "reduced" greater tuberosity is a primitive character in otariids. The relatively small diameter of the capitulum, the position of the deltoid tuberosity, and possibly the limited articular surfaces on the distal end of the humerus may also be regarded as primitive features in the otarioid pinnipeds.

The *Valenictus imperialensis* humerus is notable in that it is, relatively, the shortest and most massive humerus known among the Otarioidea. *Valenictus* is advanced and specialized in the relative shortness of the humerus, but this is accomplished by actual shortening of the shaft, and the primitive, straight posterior border of the shaft is retained. Shortening of the pinniped humerus through extreme sigmoid curvature is an advanced feature among the otariids, and is clearly exemplified in *Eumetopias* (Downs, 1956, p. 130). The acute internal angle formed by the distal end and the humeral shaft places the elbow in a more lateral position. The extreme elongation medially of the entepicondyle is related to this condition, but so many interacting factors are involved that it is impossible to analyze this condition until the scapula and forearm of *Valenictus* are discovered. The large, rounded entepicondyle indicates that the swimming mechanism was reliant on flexion and pronation of the manus (see Howell, 1929). This indicates that the *Valenictus* humerus was not specialized for unified adduction-abduction in the transverse plane, but was partially dependent on extension-flexion activities of the pectoral limb. In the living *Zalophus californianus* great and efficient speed is attained through this adduction-abduction motion of the pectoral limbs, both strokes being power strokes with little or no lost motion (Howell, 1930, p. 212; and original observations). Great leverage for the deltoid and pectoralis muscles (among others) necessary for the powerful flexion

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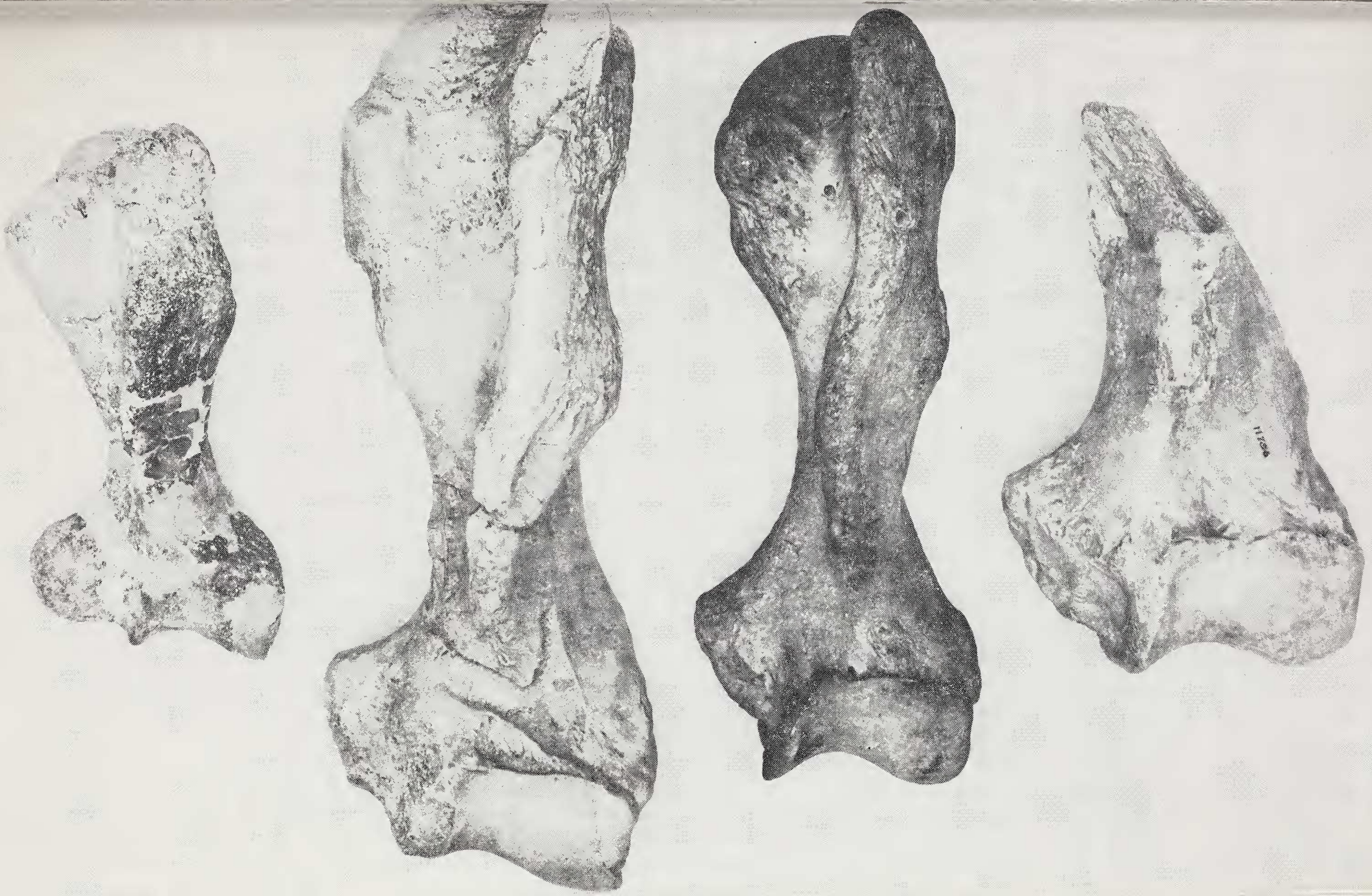
Fig. 12. Medial views (top to bottom) of left humeri of *Valenictus imperialensis*, n. gen., n. sp., LACM (CIT) 3926; *Alachtherium cretsii*, USNM 11788; *Odobenus rosmarus divergens*, USNM 200336; and *Trichecodon huxleyi*, USNM 11786. All approximately one third natural size. Photograph by Armando A. Solis.



undertaken by a pinniped with such a short brachium is provided in the *Valenictus* humerus by the extreme width, distal length, and moderate elevation of the deltoid crest. The very distal position of the entepicondyle with relation to the trochlear surfaces implies that the need for a more powerful stroke resulted in selection for short, powerful muscles to control the flexion of the manus during flexion of the limb as a whole. The relatively small diameter of the proximal capitulum, although a primitive character, would have been an advantage to a large, heavy bodied animal that spent more time in the water (although near shore) than *Odobenus*, for it would have allowed great freedom of brachial movement during a long, powerful stroke in an aquatic medium. All of this is in agreement with the idea that decrease in the length of the brachium and antebrachium with an increase in the length of the manus is a highly specialized aquatic condition (Howell, 1930, p. 218). *Valenictus* was very much specialized for an aquatic life, perhaps having been more of a truly pelagic pinniped than the modern *Odobenus*.

The probable absence of the entepicondylar foramen is not an essential point, for its presence is variable among the Phocidae (see Thomson, 1909), and in other mammals perhaps depends upon variable morphological relationships (see Landry, 1958). The presence and conformation of the deltoid tuberosity is a basic point in the recognition of odobenid affinities in the new otarioid described in this paper. Other deciding characters are: The strong medial inflection of the thick deltoid crest (found in both *Valenictus* and *Odobenus*, and not appreciably developed in any otariid genera to the exclusion of a lateral inflection); the narrowness of the bicipital groove; the obliquely directed distal end (with regard to the shaft axis); the small proximal capitulum; and the relatively straighter posterior border of the shaft.

In the late Miocene, the Atlantic coast of North America was inhabited by *Prorosmarus*, a primitive, generalized walrus. In the Pliocene, the North Atlantic was populated by essentially modern walruses of the genus *Alachtherium*. In the Pleistocene *Trichecodon* evidently occupied both sides of the North Atlantic, and *Odobenus* was well distributed in the North Atlantic and Arctic Oceans, a record even occurring in the Okhotsk Sea (Borissiak, 1930).

Valenictus imperialensis, a relatively specialized animal in at least some characters of the humerus, does not add considerably to our understanding of odobenid evolution. All that can be said with some degree of certainty is that a relatively late specialization of the odobenid stock has been documented in the general region of the supposed ancestral home of the group (McLaren, 1960). In the light of this record, it may be

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Fig. 13. Anterior views (top to bottom) of left humeri of *Valenictus imperialensis*, n. gen., n. sp., LACM (CIT) 3926; *Alachtherium cretsii*, USNM 11788; *Odobenus rosmarus divergens*, USNM 200336; and *Trichecodon huxleyi*, USNM 11786. All approximately one third natural size. Photograph by Armando A. Solis.

Table 1

Humeral measurements of fossil and Recent otarioid pinnipeds in centimeters. Approximations are in parentheses.

	Valenictus imperialensis left humerus LACM (CIT) 3926	*Odobenus rosmarus* left humerus USNM 200336	*Eumetopias jubata* left humerus LACM M550	*Allodesm* *kernens* left hum LACM 4320
Length, capitulum to a line tangent to external and internal distal trochlear edges	(24.4)	35.1	28.6	27.8
Length, proximal tip of greater tuberosity to a line tangent to external and internal distal trochlear edges	(24.9)	36.8	31.4	26.7
Length, proximal tip of lesser tuberosity to a line tangent to external and internal distal trochlear edges	(22.0)	31.9	27.7	27.2
Effective (functional) length, capitulum to most proximal concavity of trochlea	24.0	33.5	27.4	27.4
Length of deltoid crest, greater tuberosity to distal extension of rugose muscle attachment	(17.2)	(26.7)	22.0	20.3
Width of deltoid crest across deltoid tuberosity (or greatest width)	7.0	7.5	3.8	(3.3)
Greatest transverse diameter of capitulum	6.5	10.3	10.3	7.0
Anteroposterior diameter of proximal end, through capitulum and greater tuberosity	10.3	14.3	13.9	(10.9
Greatest proximal diameter of lesser tuberosity	4.5	4.1	4.2	(3.2
Least transverse diameter of shaft	4.6	5.2	5.3	3.7
Greatest width through entepicondyle and ectepicondyle	12.3	14.4	13.3	11.0
Greatest anteroposterior diameter of medial trochlear edge	5.3	8.3	7.9	5.0
Greatest anteroposterior diameter of lateral capitular edge	(4.1)	(6.4)	6.7	5.7
Width of trochlear surface at distal extremity	(6.4)	8.9	8.8	(5.5

Table 1

Humeral measurements of fossil and Recent otarioid pinnipeds in centimeters. Approximations are in parentheses.

Atopotarus courseni ht humerus	cf. *Neotherium* left humerus	cf. *Desmatophoca oregonensis* left humerus	cf. *Pontolis magnus* right humerus	*Alachtherium cretsii* left humeral cast	*Trichecodon huxleyi* left humeral cast
LACM 1376	LACM 4319	OSC V-822	LACM 4324	USNM 11788	USNM 11786
18.3	12.1	(20.3)	37.9	41.2	——
18.3	——	(20.5)	38.5	——	——
——	11.4	(19.3)	34.2	(35.0)	——
18.0	11.8	(20.0)	38.0	40.7	——
12.2	——	(13.5)	29.8	(30.3)	——
——	——	(2.6)	——	6.8	——
——	3.1	——	——	12.7	——
6.5	——	——	14.7	——	——
——	——	2.9	——	4.1	——
——	1.7	2.6	(5.0)	6.3	(8.5)
7.1	3.6	(6.7)	——	16.6	17.6
3.6	2.1	——	——	8.5	9.6
3.7	1.6	——	(6.6)	7.6	8.0
(4.1)	2.2	——	——	8.7	9.3

Table 1

Humeral measurements of fossil and Recent otarioid pinnipeds in centimeters. Approximations are in parentheses.

Table 1

Humeral measurements of fossil and Recent otarioid pinnipeds in centimeters. Approximations are in parentheses.

	Valenictus imperialensis left humerus	*Odobenus rosmarus* left humerus	*Eumetopias jubata* left humerus	*Allodesmus kernensis* left humeru	*Atopotarus courseni* right humerus	cf. *Neotherium* left humerus	cf. *Desmatophoca oregonensis* left humerus	cf. *Pontolis magnus* right humerus	*Alachtherium cretsii* left humeral cast	*Trichecodon huxleyi* left humeral cast
	LACM (CIT) 3926	USNM 200336	LACM M550	LACM 4320	LACM 1376	LACM 4319	OSC V-822	LACM 4324	USNM 11788	USNM 11786
Length, capitulum to a line tangent to external and internal distal trochlear edges	(24.4)	35.1	28.6	27.8	18.3	12.1	(20.3)	37.9	41.2	—
Length, proximal tip of greater tuberosity to a line tangent to external and internal distal trochlear edges	(24.9)	36.8	31.4	26.7	18.3	—	(20.5)	38.5	—	—
Length, proximal tip of lesser tuberosity to a line tangent to external and internal distal trochlear edges	(22.0)	31.9	27.7	27.2	—	11.4	(19.3)	34.2	(35.0)	—
Effective (functional) length, capitulum to most proximal concavity of trochlea	24.0	33.5	27.4	27.4	18.0	11.8	(20.0)	38.0	40.7	—
Length of deltoid crest, greater tuberosity to distal extension of rugose muscle attachment	(17.2)	(26.7)	22.0	20.3	12.2	—	(13.5)	29.8	(30.3)	—
Width of deltoid crest across deltoid tuberosity (or greatest width)	7.0	7.5	3.8	(3.3)	—	—	(2.6)	—	6.8	—
Greatest transverse diameter of capitulum	6.5	10.3	10.3	7.0	—	3.1	—	—	12.7	—
Anteroposterior diameter of proximal end, through capitulum and greater tuberosity	10.3	14.3	13.9	(10.9)	6.5	—	—	14.7	—	—
Greatest proximal diameter of lesser tuberosity	4.5	4.1	4.2	(3.2)	—	—	2.9	—	4.1	—
Least transverse diameter of shaft	4.6	5.2	5.3	3.7	—	1.7	2.6	(5.0)	6.3	(8.5)
Greatest width through entepicondyle and ectepicondyle	12.3	14.4	13.3	11.0	7.1	3.6	(6.7)	—	16.6	17.6
Greatest anteroposterior diameter of medial trochlear edge	5.3	8.3	7.9	5.0	3.6	2.1	—	—	8.5	9.6
Greatest anteroposterior diameter of lateral capitular edge	(4.1)	(6.4)	6.7	5.7	3.7	1.6	—	(6.6)	7.6	8.0
Width of trochlear surface at distal extremity	(6.4)	8.9	8.8	(5.5)	(4.1)	2.2	—	—	8.7	9.3

useful to reconsider the possibility of odobenid migration from the North Pacific to the North Atlantic by way of a late Miocene Central American seaway, although McLaren considers this “climatically unlikely.” The geographic position of the *Valenictus* discovery would seem to indicate that the genus might represent a relic group of early odobenids, but until further elements, especially cranial bones, are found such speculation is somewhat conjectural.

SUMMARY AND CONCLUSIONS

A new genus and species of pinniped is described on the basis of a nearly complete humerus from early Pliocene sediments in south central California. A complete survey of odobenid and otariid humeri, both fossil and Recent, is made in conjunction with this description.

The new genus and species, *Valenictus imperialensis,* is a pinniped: The humerus follows the general plan of Recent and fossil pinniped humeri in the large deltoid crest, short shaft, and pronounced tuberosities. Cetacean, sirenian, and desmostylian humeri in no way approach that of *Valenictus.*

Valenictus imperialensis is an odobenid because (1) a deltoid tuberosity is present on the type humerus, (2) all other humeral characters found in *Valenictus* and not present in odobenids are not present in otariids, (3) the apparent locomotory mechanisms resemble those of modern walruses, and (4) it exhibits other humeral adaptations which would have allowed it to occupy an environment similar to, but possibly more pelagic than that habituated by modern walruses.

Valenictus imperialensis represents an early specialization of a primitive otarioid stock because (1) it retains the primitively straight posterior border of the shaft, (2) the capitular axis-shaft axis angle is smaller than that in most other living or fossil otarioids, a primitive character, (3) the entepicondyle is larger and more specialized than that of other otarioids, differing significantly in shape and position, and (4) the humerus is relatively the shortest and most massive of any otarioid—another specialization. Other specialized conditions are noteworthy, most especially the very proximal position of the deltoid tuberosity.

The humeri of *Allodesmus* and *Atopotarus* are very similar, and in this respect suggest that the two animals may be closely related. However, final word on their relationship will have to await study of comparable cranial elements.

A humerus is herein described and designated as cf. *Neotherium.* Both this humerus and that of the cf. *Desmatophoca oregonensis* referred to in this report follow the same basic structural plan, and this suggests a phyletic relationship.

The humerus of *Alachtherium cretsii* presents an intermediate structural grade between the typical otariid humerus and that of *Odobenus* and *Valenictus* in the shape and position of the deltoid tuberosity.

Downs’ (1955) referral of a pinniped from the San Joaquin Hills